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The impact of climate-change induced temperature increases on the suitability of street tree species in California (USA) cities

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ABSTRACT

Climate change, resulting in increased temperatures, has the potential to alter the species composition of urban tree populations. We examined the likely changes in composition of common street tree species in California (USA), using a space-for-time substitution approach which paired each of the 16 cities covering the climatic range of the state ("representative city") with a "warm city" counterpart, where the climate of today approximates the climate of the representative city in 2099. Of the 140 tree species found, as many as 82 species may be unsuitable for the future warmer climate. This change is geographically non-uniform, with greater losses (up to 100% of common species unsuitable for future climate) found in cities away from the ocean coast. In contrast, assessing climate suitability of tree species from published sources (professional judgement, resulting in implied climate envelopes), reduces the number of unsuitable species to as few as 14, although a hybrid approach that accounts for the substantial gaps in the climate envelope information results in an estimated 55 unsuitable tree species. The difference between the observed and estimated results (82 unsuitable species vs. 55) is likely caused by the climate envelope information insufficiently accounting for the irrigation needs of newly-planted street trees in the Mediterranean-type climates like California. Our results demonstrate the viability of the space-for-time substitution approach for evaluating possible climate change effects on urban trees, and suggest both an immediate need to re-evaluate the planting palette of street trees, and a long-term imperative to trial new tree species.

1. Introduction

Anthropogenic climate change ("global warming") is contributing to higher temperatures in urban areas, and in temperate climates these increases are especially notable during summers. In 2016, the globally averaged temperature over land and ocean surfaces was the highest since records began in 1880, and the warmest July in 136 years of modern record-keeping was recorded (NOAA, 2017). In California (USA), the average maximum temperature has increased over the past century, with the increase ranging from 0.9 °C to 1.4 °C (1.6–2.5 °F; Lynn, 2015). Projections of climate warming in California indicate further increases in average July average maximum temperatures, projected to range from 2.5 °C (4.6 °F) in Santa Ana, a coastal city in Southern California, to 7.2 °C (13 °F) in the inland city of Barstow (Cal-adapt, 2014). Along with these increasing temperatures, models project a decrease in average annual precipitation and snow accumulation in parts of California, (Diffenbaugh et al., 2015) ranging from -20.3 mm (-0.8 in.) in the northern city of Ukiah, to -162.6 mm (-6.4 in.) in the central-interior city of Stockton (Knowles et al., 2006). These projected reductions are substantial, as they would represent losses ranging from 1% to 42.7% of the current precipitation, respectively (Cal-adapt, 2014).

These changes are potentially impactful on urban environments, as most of California's population and large cities (e.g., Los Angeles, San Diego, San Jose, Sacramento) are located in Mediterranean-type climates. Characterized by warm-to-hot dry summers, and mild and wet winters (Koppen types Csa, Csb, and Csc; Kottek et al., 2006), the climates of the southern half of California – and the largest cities of Los Angeles, San Diego, and San Jose (combined population of about 20 million) – are also characterized by their potential evapotranspiration exceeding their annual precipitation (e.g., Sanford and Selnick, 2013). Yet, in contrast to the natural vegetation that is xeric or drought-tolerant in the southern and central parts of the state, the current street tree palette across California cities includes many temperate-climate trees (e.g., Ritter, 2011; Thompson, 2006). Some of these urban tree species may be only partially adapted to the current climate, and may

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require supplemental water, either during their establishment phase, or throughout their life. Thus, a climate with increasing temperatures and decreasing precipitation is likely to have substantial, negative impacts on commonly planted street tree species in California, depending on each species' adaptation to these new environmental conditions. Physiological changes such as early defoliation and reduced growth can be expected for some species, while others may suffer mortality or fail to break dormancy in spring (Coder, 1999; Tadewaldt, 2013). In turn, these responses by individual trees would be reflected as composition changes in street tree populations. Potential for this effect was observed by the authors during the recent 2013–2016 drought, when below-average precipitation accompanied by reduced availability of water for irrigation of street trees resulted in visible deterioration in street tree condition. This decline was notably varied, both spatially across the state, and across tree species within individual cities, suggesting that the that effects of climate change on street tree populations might be strongly influenced by the interactions of local climate (and its projected change) with the local composition of street tree species, at least in California.

Concerns over such effects of global warming have led to efforts to estimate the suitability of ornamental landscape species, including trees, to future climates and to provide planting guidance to practitioners. For example, a plant heat zone map for the United States was created by the American Horticultural Society (American Horticultural Society (AHS, 1997; LaLiberte, 2016), with heat zones defined by the yearly number of "heat days" (daily max. temp > 30 °C or 86 °F). However, the listed examples of plants that perform well in each heat zone do not include commonly used street trees. Conversely, Buley and Cregg (2016) stressed the need for urban tree selection with a view toward the changing climate, and suggested – based on the general understanding of species' physiology and phenology – increased use of species from more phenotypically plastic genera such as *Acer, Gymnocladus, Nyssa, Plantanus, Taxodium,* and *Ulmus.* Similarly, in California, a limited number of publications include professional opinions on the adaptation of trees to California landscape regions (Brenzel, 2007; Perry, 2010; Selectree, 2016), and professional consensus on the relative water requirements of common landscape plants (Costello and Jones, 2014). While these publications represent valuable sources of information for judging the adaptation of tree species to a warming and drying climate, they do not substitute for systematic evaluation of tree performance. At least one such study that includes growing novel species and cultivars and evaluating their performance in several cities across California is currently in progress (McPherson et al., 2018), but the results will not be known for many years.

Alternative approaches have been proposed for evaluating plant performance in changing climate and predicting effects of climate change on natural ecosystems (e.g., Anacker et al., 2013). Broadmeadow and colleagues proposed in 2005 that to maintain timber production in a changing climate, "provenances from regions with a current climate similar to that predicted for the future for a given site should be selected" (p. 157), and in 2013 Blois et al. suggested that "space-for-time substitution" method, commonly used in studies of plant succession (Pickett, 1989), may be useful in predicting climate-change effects on biodiversity. In urban forests, a range of approaches to evaluating the effect of climate change on tree populations has been used. These include relatively simple approaches based on the trees' "climate envelope" (i.e., the set of climatic constraints on a species' distribution) focusing on climate variables and projected pest problems in a changing climate (e.g., Yang, 2009). But the approaches also include increasingly more complex analyses, such as when various management considerations are explicitly included (e.g., Ordóñez and Duinker, 2014, 2015), and becoming even more involved when social considerations and larger-scale constraints are introduced (e.g., Brandt et al., 2016). Brandt et al. (2017) applied the framework they developed (2016) to the urban forests in the Chicago region. Their analysis combined a modeled climate envelope for native trees, together with a tolerance of heat and cold for non-native trees (as indicated by AHS Heat Zones and USDA Hardiness Zones) with assigned scores for adaptability to pests and diseases. The results of their analysis produced two vulnerability categories (low; high) of tree species in the Chicago area to climate change. Yet, none of the studies have been carried out in Mediterranean-type climates, where decreased water and increased summer heat are likely to be significant constraints in the changing climate.

This work presents the first use of the space-for-time substitution method to evaluate the potential impact of climate change on street tree populations. We assess the composition of common street tree species in California cities, to identify the common species that would be expected to perform poorly or would fail to survive in the warmer climate. We also briefly compare the output of the space-for-time substitution to the results of professional opinion in predicting the future suitability of street tree species.

2. Methods

To simulate the predicted temperature conditions in California cities in year 2099, we adopted the space-for-time substitution (Pickett, 1989) as our principal conceptual method. In brief, we compared the most common street tree species occurring in a city representative of each of the 16 California climate zones ("representative city") to tree species in a city that is currently as warm as the representative city is predicted to become by 2099 ("corresponding city", or "warm city"). Those common tree species in representative cities that are absent from the warm cities are deemed unsuitable for the warmer/drier future climate. The evaluation comprised the following six steps.

2.1. Selecting representative cities

To identify representative cities in each of the 16 California climate zones (California Energy Commission, 2015) three to five cities in each zone were selected for initial screening, in locations typical of the geography of the climatic zone and large enough (> 25.9 km^2, i.e. 10 mi^2) to have a substantial street tree population, with exceptions for those climate zones without any large cities. For the selected cities, we averaged the historic (1961–1990) average maximum July temperatures (Western Regional Climate Center, 2013), and the city whose average maximum July temperature was closest to the average for the climate zone was selected as the representative city for that zone.

2.2. Modeling future temperature in representative cities

To predict the average maximum July temperature in 2099 for each representative city, we averaged three temperature projections (HadGEM2-ES, CNRM-CM5, CanESM2) based on four greenhouse gas emission scenarios (spanning the range from RCP 4.5 to RCP 8.5) from the Cal-Adapt model (2099 is the final year covered by the Cal-Adapt model; Table 1). Our selection of the July maxima as the relevant climate metric reflects the concept of heat tolerance of trees, based on the work of Ball et al. (1995), Yamada et al. (1996), Kitao et al. (2000), and Weng and Lai (2005). As we are not using the climate information to develop a bioclimatic envelope for trees, but simply to select corresponding cities, the July maximum represents both a biologically-relevant and parsimonious metric to guide this selection.

2.3. Selecting corresponding cities (warm cities)

To enable assessment of the effect of increased temperatures on street tree populations, we identified for each representative city a corresponding city whose historical average maximum July temperature approximates the future temperature projected for the representative city in 2099. For example, Yuba City was selected as the corresponding city for King City because the projected average

Table 1
Representative cities for each California climate zone (historic temps. from: Western Regional Climate Center, 2013; predicted temps. from Cal-adapt, 2014). The city whose current climate approximates the future climate of the representative city in year 2099 is termed "corresponding city" (or "warm city").

ClimateZone	Representative City	Historic July Avg. Max. °C (°F)		2099 Predicted July Avg. Max. °C (°F)		Corresponding City
1	Eureka	16.6	(61.9)	20.5	(68.9)	Berkeley
2	Ukiah	32.1	(89.7)	35.7	(96.2)	Fresno
3	Berkeley	21.3	(70.3)	26.9	(80.4)	Santa Ana
4	King City	29.8	(85.7)	34.3	(93.7)	Stockton
5	Santa Maria	24.6	(76.3)	26.9	(80.4)	Santa Ana
6	Santa Monica	21.4	(70.5)	27.8	(82.0)	King City
7	San Diego	23.3	(74.0)	28.8	(83.8)	Santa Ana
8	Santa Ana	27.9	(82.3)	30.5	(86.9)	Burbank
9	Burbank	30.1	(86.2)	35.1	(95.2)	Fresno
10	Riverside	33.3	(91.9)	38.2	(100.8)	Barstow
11	Yuba City	34.2	(93.5)	41.5	(106.7)	El Centro
12	Stockton	32.4	(90.4)	38.7	(101.7)	Barstow
13	Fresno	35.3	(95.5)	42.2	(107.9)	El Centro
14	Barstow	37.5	(99.5)	44.7	(112.5)	El Centro
15	El Centro	41.1	(106.0)	46.4	(115.6)	Furnace Creek
16	Susanville	31.5	(88.7)	36.5	(97.7)	Barstow

maximum July temperature for King City is 34.3 °C (93.7 °F) and the historic average maximum July temperature in Yuba City was 34.2 °C (93.5 °F). In other words, Yuba City of today approximates King City of 2099 (Yuba City = warm King City). We were thus able to use the same city twice – once as a representative city, and again as the warm city for a city in a cooler climate zone; the only exception was the warmest climate zone (representative: El Centro; 46.4 °C or 115.6 °F projected July maximum), for which we had to identify a warm city (Furnace Creek; 46.3 °C or 115.3 °F current maximum) that itself does not have a corresponding city (Table 1).

2.4. Street tree surveys

We sampled public street trees in each of the 16 cities and Furnace Creek in 2015 and 2016. We located the sampling points by overlaying a cardinally-oriented grid on a map of each city, with the grid cell size determined by the size and shape of the city to ensure that the random sample points could be located from across the entire city area. Fifty grid-line intersections were randomly selected, and the road intersection nearest to each selected grid point was designated a sampling point. At each sampling point (road intersection), four 30.5 m (100 ft.) plots were laid out, one along each street leading away from the intersection, producing 200 sampling plots (except in some cities, where three-way intersections occurred, resulting in slightly fewer plots). Each plot included trees in the parkway strip, and in the median (if present). On streets without parking strips, species of trees within 3.05 m (10 feet) of the sidewalk were recorded, and if sidewalks were absent, then species of trees within 3.05 m of the curb were recorded. We designed the sampling plots based on the typical public right-of-way, which in California cities extends 3.05 m from the edge of sidewalk or roadway, and thus the trees planted in the sampled space could be presumed to be publicly-planted street trees.

2.5. Species frequency calculation and commonly planted species designation

To determine the common street tree species in each city, we started by sorting our species lists by the frequency of occurrence (in each city), defining the frequency as the percentage of sample plots on which a tree species occurred (e.g., if *Sequoia sempervirens* were found on 25 of the 200 plots, its frequency of occurrence would be 12.5%). We defined "commonly planted street tree species" as those occurring in the ten highest-ranked frequencies. Note that this approach often produced more than ten commonly planted tree species in a single city, as multiple species could have the same frequency of occurrence (e.g., if in the ten highest-ranked frequencies two species had the same frequency, then both species would be included, resulting in eleven total species).

2.6. Comparing the commonly planted species in representative cities and warm cities

To estimate which species would not survive or perform well as the climate becomes warmer and drier, we compared the commonly planted street trees in each representative city with (a) those in their respective corresponding city (warm city) as well as in (b) all cities with climate warmer than the corresponding city. We deemed the trees absent from the warm city and all other warmer cities unlikely to survive in the representative city in the future. Including all the warmer cities (step b) is intended to correct for the possibility that a tree species is absent from the warm city for reasons other than climate; if, however, a tree species absent from the warm city was found in an even warmer city, then we would restore it to the list of future-suitable trees.

Finally, a combination of two additional adjustments, which we term "professional opinion," were applied to the list of trees to assess their temperature tolerance and water needs. First, we used a published source (Perry, 2010), and interviews with local tree experts to evaluate the temperature-tolerance of 10 common species found in the three hottest locations (Barstow, El Centro, and Furnace Creek) that were absent from literature. Second, we compiled the estimated water needs of all commonly used street tree species (WUCOLS IV, based on a professional consensus; Costello and Jones, 2014); we noted any species that WUCOLS had listed as unsuitable (for the warm city) or that had scored high in its water needs (a potential problem under future conditions of uncertain irrigation availability). Where WUCOLS data were unavailable, we assigned the species "medium" water-use rating (occurred only once). The professional opinion filter could cause a tree species to either be removed from the space-for-time-substitution future-suitable list or it could cause a previously-removed species to be reinstated.

3. Results

A total of 140 species were identified in the survey. Species richness in representative cities ranged from 28 in El Centro to 85 in Ukiah (mean: 54; Table 2, col. 1), and only ten tree species were recorded in Furnace Creek. Species richness displayed no obvious geographic trends, except that it was lower in the desert regions (climate zones 14 and 15). Importantly, species richness appeared to be unrelated to either a city's latitude or its proximity to the ocean coast (mean species richness was 19, 24, and 19 for coastal, coastal-proximate, and inland

Table 2
Summary of the number of (**1**) most frequently used tree species, (**2**) tree species not found in warm and warmer cities (superscript indicates the number of species, included in total, whose absence may be caused by cold sensitivity), (**3**) are unsuitable for future climate according to the professional opinion contained in the Perry and WUCOLS references.

Climate Zone	City	(1) in 10 most frequent ranks,		(2) absent from "warm city" or warmer cities		(3) in column 2, that are ill-suited to future climate according to Perry/WUCOLS	
		Count	(Total)	count	%	count	%
1	Eureka	29	(52)	0	0	0	0
2	Ukiah	23	(85)	9	39	2	9
3	Berkeley	20	(66)	2	10	0	0
4	King City	25	(57)	2	8	0	0
5	Santa Maria	17	(49)	0	0	0	0
6	Santa Monica	14	(59)	1	7	1	7
7	San Diego	25	(60)	0	0	0	0
8	Santa Ana	12	(41)	0	0	0	0
9	Burbank	23	(50)	8^1	35	3	11
10	Riverside	16	(60)	10^1	63	9	56
11	Yuba City	15	(73)	15	100	11	73
12	Stockton	13	(64)	6	46	4	31
13	Fresno	32	(57)	19	59	17	53
14	Barstow	15	(31)	9	60	3	20
15	El Centro	10	(28)	7^1	70	3	30
16	Susanville	34	(41)	34	100	29	85

cities, respectively). A total of 75 species were classified as species of common occurrence (i.e., occurring in the top ten frequency ranks), but the number of species that made up the ten ranks varied (mean: 20 species). In some cities, a repeated planting of a few species resulted in a limited number of ten-most-frequent-ranked species (e.g., Stockton: 13 top-ten-ranked species out of 64; Santa Monica: 14 out of 59 species; Table 2, col. 1). In other cities, the frequency of occurrence of individual species was low, resulting in a greater number of species occurring in the top ten frequency ranks (Eureka: 29 out of 52 species were found in the top ten frequency ranks; Fresno: 32 out of 57 species).

The most frequently observed species were *Lagerstroemia indica* (found in 11 of the 16 cities), *Liquidambar styraciflua*, *Magnolia grandiflora*, and *Platanus* × *hispanica* (each found in 12 of the 16 cities). In contrast, several species were recorded in only a single city, e.g., *Casuarina cunninghamiana* in El Centro, *Chilopsis linearis* in Barstow, and *Quercus hemisphaerica* in Fresno.

When the lists of common street tree species in a representative city were compared to the lists of all tree species occurring in its corresponding city and the warmer cities (Table 2, col. 2; Fig. 1), one of three patterns emerged:

(1) all tree species in a representative city also occurred in its corresponding city or warmer cities (this pattern was found in 4 cities: Eureka, Santa Maria, San Diego and Santa Ana (Zones 1, 5, 7 and 8, respectively), or
(2) a portion of the commonly occurring tree species in a representative city did not occur in its corresponding city or warmer corresponding cities (pattern found in 10 cities, e.g., as in the case of Ukiah), or
(3) none of the commonly occurring tree species in a representative city occurred in its corresponding city or warmer corresponding cities (pattern found in Yuba City and Susanville; Fig. 1).

While the last pattern could be attributed to situations where particular species occur only once as a common street tree (e.g., *Acer saccharum* in Ukiah, *Cercis canadensis* in Stockton, *Sophora japonica* in Berkeley), this same pattern nevertheless was observed in species that occurred 3 or more times, i.e., in 3 or more cities (3 cities: e.g., *Betula pendula*, *Fraxinus uhdei*, *Prunus cerasifera*, *Quercus rubra*, *Sequoia sempervirens*; 4 cities: *Lagerstroemia indica*, *Magnolia grandiflora, Pyrus calleryana* 'Bradford'; 5 cities: *Liquidambar styraciflua, Platanus x hispanica*).

A total of 82 species was identified as likely unsuitable for future climate using the space-for-time substitution (Table 2, col 2; Table 3). Broadleaf dicots dominate the not suited list (66 species), followed by conifers (13 species, including *Ginkgo biloba* and *Afrocarpus gracilior*), but three species of palms are also included. Thirty-three families are represented, with *Fabaceae* (8 species), *Sapindaceae* and *Pinaceae* dominating (6 species) followed by *Oleaceae* and *Myrtaceae* (5 sp. each), and *Rosaceae* and *Cupressaceae* (4 species each). *Liquidambar styraciflua* and *Platanus* x *hispanica* occur on the not suited list for five cities, whereas *Fraxinus angustifola* 'Raywood,' *Magnolia grandiflora*, and *Pyrus calleryana* 'Bradford' are each identified in four cities. In contrast, several species expected to be ill-suited for future climates were found in a single city, e.g., *Acacia dealbata* found only in El Centro, *Cassia leptophylla* in Burbank, *Ginkgo biloba* in Fresno.

Comparing the space-for-time substitution results for individual species with that of the professional opinion (of Perry/WUCOLS and the interviews in the three warmest cities), the latter generally forecasts a smaller range of climate zones where an individual species is expected to fail. Thus, the total count of tree species deemed unsuitable by professional opinion (Table 2, col. 3) is greatly reduced in comparison to the space-for-time substitution, to as few as 14 species, because the Perry/WUCOLS adjustment restores species from each city's not suited list back to suited status (ranging from 1 to 8 species restored; Table 3). The only notable exception to this pattern is with *Magnolia grandiflora* that Perry would expect to become unsuitable for planting in zones 3 and 4.

To make this large list of potentially-unsuitable trees (Table 3) more accessible to the practicing arborist, we highlight in Table 3 in boldface those species that in our estimation are most likely to perform poorly in the future, those species that (1) either were found unsuitable in multiple cities (e.g., *Liriodendron tulipifera*), or (2) were modeled as unsuitable by both the space-for-time substitution and by the Perry/WUCOLS professional opinion (e.g., *Afrocarpus gracilior*). Notably, this procedure (itself another form of professional opinion) reduces the list to 55 species.

4. Discussion

This analysis indicates that in some cities a substantial proportion of the now-common street tree species is potentially unsuited to the changing climate. This finding is notable in two aspects, first in the diversity of species that could potentially become unsuitable for planting in some cities, and second in the uneven geographic distribution of this failure.

The potential span of locally-unsuitable trees – possibly up to 82, but likely no less than 55 species – represent a substantial fraction of common urban species identified by Ritter ("about 150"; 2011, p. xiv), and include some species that are nearly ubiquitous in California's cities, such as *B. pendula,* L. *styraciflua*, *P. x hispanica*, *P calleryana*, and *S. sempervirens*. Although some of these are disfavored at present (e.g., *L. styraciflua* – now avoided for its pavement-damaging roots; McBride and Jacobs, 1976), they remain prominent in many low-density residential neighborhoods as a result of past planting patterns, and their loss would be immediately noticeable. Conversely, of the species in the Table 3, only three (*Dictyosperma album*, *Quercus hemisphaerica*, and *Senna surattensis*) could be considered unusual, as they are not listed in Ritter's 2011 book; yet even these three species may be locally common and their loss important in some cities.

We emphasize that our results do not indicate that all of these species will be lost from all cities, but suggest that their status as reliable urban species must instead be evaluated in each city, with a view

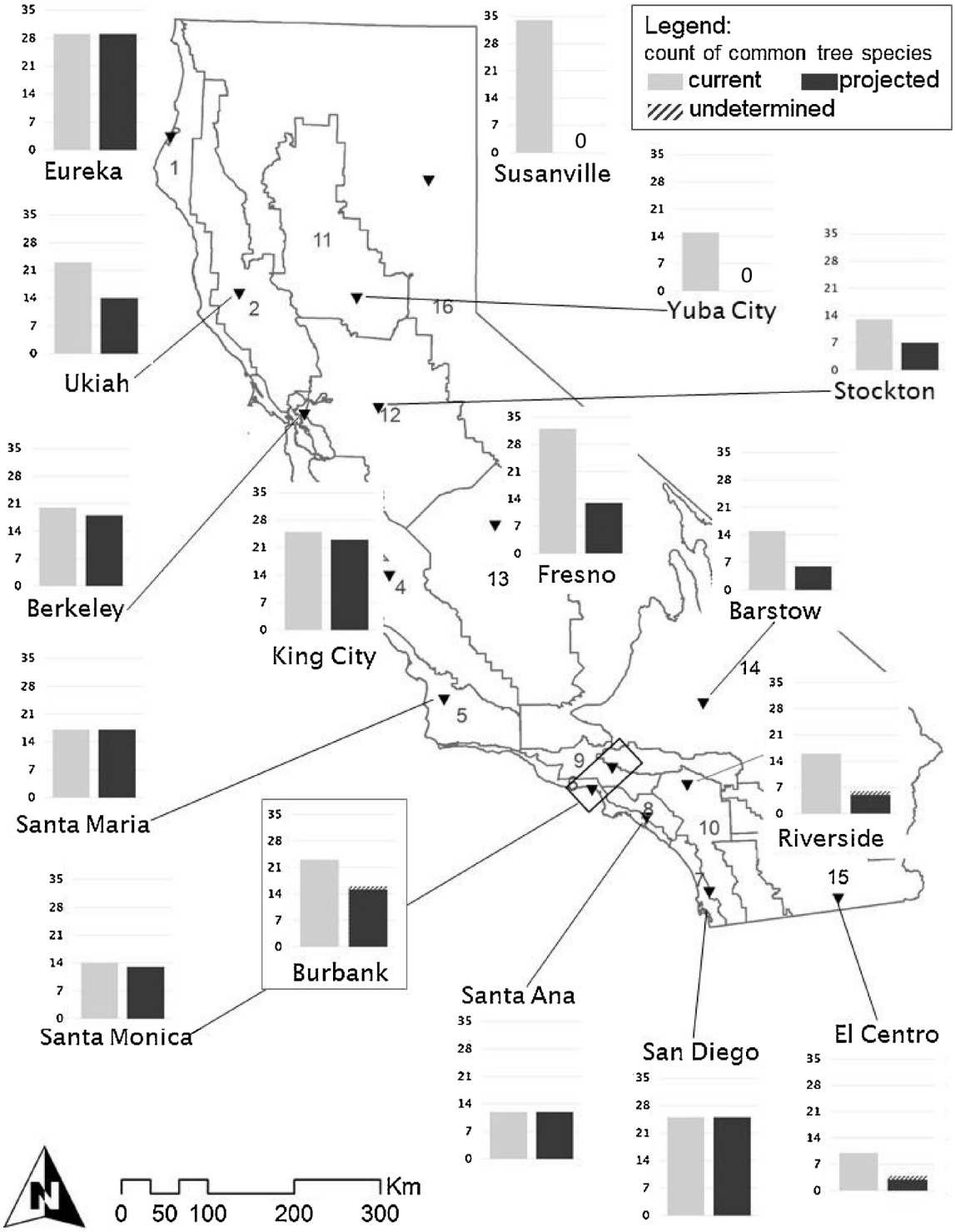

Fig. 1. Study sites, shown within their respective climate zones (numbered 1–16). For each city, the count of common tree species is shown ("current" count), together with the count of species occurring in warmer cities, representing the future condition ("projected" count). "Undetermined" refers to any species whose current absence from a "warm" city could have been due to cold-sensitivity (as in Burbank, Riverside, and El Centro; one species remains "undetermined" in each city).

to the warming climate.

This is because the potential loss of species appears to be remarkably non-uniform across California, and climate change effects on street trees do not follow the north-south gradient of temperature and potential evapotranspiration. Instead, the cities where street tree diversity is most likely to diminish are inland, away from the Pacific coast but located at all latitudes, in the Central Valley (climate zones 11–13), the Southern and Northern interior valleys and mountains (zones 9,10, and 16), and the southern deserts (zones 14 and 15). The areas most at risk for tree loss exclude a substantial part of three metropolitan centers (the City of San Diego, the San Francisco Bay Area, and coastal parts of Los Angeles), but include almost all the other major urban areas in California, including the populous inland portions of the Los Angeles basin and the San Diego basin, as well as the inland cities throughout

Table 3
Unsuitable species, based on absence from warmer cities (-), or professional opinion either by Perry (P) or WUCOLS ("!" indicates a rating of "unsuitable" or "high" in the water-use category). Highlighted in boldface are species (n = 55) for which multiple lines of evidence suggest future unsuitability (either the species is absent from multiple cities, or the professional opinion of unsuitability coincides with absence from a city). Because no species From Eureka, Santa Maria, San Diego and Santa Ana (Zones 1, 5, 7 and 8) were absent from their corresponding cities, those Zones are omitted from this table.

Species	Climate Zone/Representative City												Number of Climate Zones
	2	3	4	6	9	10	11	12	13	14	15	16	
	Ukiah	Berkeley	King City	S. Monica	Burbank	Riverside	Yuba City	Stockton	Fresno	Barstow	El Centro	Susanville	
Acacia dealbata											– !		1
Acer negundo												–	1
Acer platanoides		!										–	2
Acer rubrum							–					–	2
Acer saccharum	–											–	2
Aesculus hippocastaneum												– !	1
Afrocarpus gracilior									– !				1
Ailanthus altissima										–			1
Arbutus 'marina'			–										1
Betula pendula	– P	!	P	!			–					–	4
Brachychiton populneus									–				1
Broussonetia papyrifera												–	1
Camellia japonica					– P								1
Cassia leptophylla					–								1
Casuarina cunnnighamiana												–	1
Catalpa speciosa	–											– !	1
Cedrus deodara									–				1
Celtis occidentalis	P							–					2
Cercis canadensis						– P							1
Chilopsis linearis										–			1
Cinnamomum camphora									–				1
Corymbia citrodora											– !		1
Crataegus douglasii												– !	1
Crataegus laevigata												– !	1
Dictyosperma album									–				1
Eucalyptus cinerea											–		1
Eucalyptus robusta					–								1
Ficus microcarpa					–						–		2
Fraxinus 'Raywood'						–	–		–			–	4
Fraxinus latifolia	–												1
Fraxinus uhdei							–			–			2
Fraxinus velutina											–		1
Geijera parviflora											–		1
Ginkgo biloba									– P				1
Gleditsia triacanthos	–											–	2
Hesperocyparis macrocarpa												– !	1
Jacaranda mimosifolia						– !							1
Juglans californica												– !	1
Juglans regia												– !	1
Juniperus osteosperma										–		–	2
Koelreuteria paniculata												– P	1
Laburnum x watereri						– !							1
Lagerstroemia indica						–	–	–	–				3
Ligustrum japonicum	–												1
Liquidambar styraciflua						–	–	–	–			–	5
Liriodendron tulipifera					–							–	2
Lophostemon confertus										–			1

(*continued on next page*)

Table 3 (*continued*)

Species	Climate Zone/Representative City																				Number of Climate Zones
	2		3		4		6		9		10		11			12		13		14	15	16		
	Ukiah		Berkeley		King City		S. Monica		Burbank		Riverside		Yuba City			Stockton		Fresno		Barstow	El Centro	Susanville		
Magnolia grandiflora			P		P						–		–		!	–		–					!	7
Melia azedarach																				–				1
Morus alba													–					–		–				3
Picea abies																						–	!	1
Picea pungens																						–		1
Pinus halepensis																				–				1
Pinus radiata																		–	!					1
Pinus sylvestris																						–	!	1
Pistacia chinensis													–											1
Pittosporum undulatum			–																					1
Platanus racemosa																						–	!	1
Platanus x hispanica											–	!	–	P	!	–	!	–	!			–	!	5
Podocarpus macrophyllus									–															1
Populus alba																						–	!	1
Populus fremontii																						–	!	1
Prunus cerasifera	–												–	P								–	P	3
Pyrus 'Bradford'													–	P		–		–				–	P	4
Quercus agrifolia	–								–															1
Quercus hemisphaerica																		–						1
Quercus rubra													–					–				–		3
Robinia pseudoacacia																		–				–		2
Salix matsudana 'Tortuosa'																						–	!	1
Schinus polygamus					–																			1
Senna surattensis									–	!														1
Sequoia sempervierns		!				!					–	!	–		!			–	!					6
Sophora japonica			–																					1
Syagrus romanzoffiana													–											1
Thuja occidentalis																						–		1
Tilia cordata																						–	!	1
Trachycarpus fortunei											–	P												1
Triadica sebifera																		–	!					1
Tristaniopsis laurina							–																	1
Ulmus parvifolia																				–	P			1
Ulmus pumila																					–			1
Umbellularia californica	–																							1
n=82																								

central California. The population in these inland areas is expected to continue growing (State of California, 2016), as these areas offer space for residential development that is no longer available on the coast. Yet, the tree managers in these new cities are unlikely to find the additional irrigation water that might be needed in a warmer/drier climate, nor the additional funds needed for irrigation infrastructure. Thus, a short-term response in these climate zones may involve removing from new planting plans the tree species identified as poorly-performing in the future. Yet, this suggestion might be difficult to implement, given that the current performance of these tree species may be satisfactory. In contrast, it is also probable that increased winter-minimum temperatures may lead to some currently cold-sensitive species to become suitable for planting. However, the magnitude of this effect is unclear, as is the availability of those tree species, and this effect would not negate the loss of the currently-common trees, although it could over time compensate for it.

It is interesting to consider an emergent aspect of our results: the traits of the affected species. Although a detailed examination is beyond the scope of the present study (but has been used before, e.g. NatureServe CCVI 3.02; NatureServe, 2015), some trends can be compared to previous works. For example, Buley and Cregg's (2016) suggestion of preferring genera with demonstrated phenotypic plasticity seems helpful (as they might include climate-adaptable traits), yet we found species of *Acer* and *Platanus* – two of the genera listed for their plasticity – to be potentially unsuitable. Nevertheless, only a limited range of species from those two genera appear in our list, and the more heat-tolerant *Acer* and *Platanus* species might perform well. In general, heat seems to be one important factor, both an individual species' tolerance to heat stress and a city's likelihood of experiencing increasing heat. The response of plants to heat has been studied from the beginning of plant ecology when heat was identified as one of the principal factors affecting the distribution of plants (Warming, 1909), to the works of Meyer and Anderson (1939), Kramer and Kozlowski (1960) and Vierling (1991). In arboriculture, from the early work of Coder (1999) on heat and trees, to the recent study by Meineke et al. (2016) using higher temperatures in urban heat islands as surrogates for the impact of global warming on street trees, findings indicate that increasing urban temperatures result in decreased photosynthesis and tree growth, and in elevated incidence of pests.

An even more deleterious effect is seen when drought and heat co-occur, although no specifically urban studies are available. Nevertheless, both Mittler's (2006), review of the relationship between drought and heat stress in plants, as well as U.S. Forest Service's comprehensive study of drought in the forests of the United States (Vose et al., 2015), reveal consistently negative effects of the combination of heat and drought. Because of the strong rainfall seasonality in nearly all of California's larger cities (i.e., dry summer months, May-September), many urban tree species have little chance of establishing unless they are irrigated for at least the first year after planting. Climate change could both extend this period of required irrigation and necessitate larger irrigation volumes, a combination that could be remedied in practice (by irrigation), but is not readily-accounted-for in the climate envelope models. In contrast, the method presented here implicitly accounts for the effects of management, by comparing *actual* urban forests of different cities, and thus could usefully complement the other climate change evaluation approaches (climate envelopes and professional judgement). We propose that the large difference seen in this study between the results of the professional judgement-based models of Perry and WUCOLS, and the space-for-time substitution approach is, at least in part, accounted for by irrigation. Namely, the professional opinion was more optimistic in assigning species suitability, because it likely included the implicit expectation that the water needs of trees will be met with supplemental irrigation where necessary. Yet, the space-for-time substitution reveals a considerably narrower palette of trees, possibly suggesting that the water limitations are not as easily remedied in practice. In Mediterranean climate, more research on this point is needed.

Finally, the issue of irrigation and horticultural management in general, warrants a brief discussion of the utility of our study method in complementing other approaches to evaluating climate change effects on urban tree populations. First, this method is conceptually different from than the "climate envelopes" approach of, e.g., Yang (2009), or those used in part by Brandt et al. (2016, 2017). It could thus be a useful complement in situations where climate envelopes are unknown (or unpublished), as is the case for many ornamental trees (noted by both Yang (2009) and Brandt et al. (2017)). Similarly, the climate envelopes approach presumes that most of the mechanisms that limit tree species distribution in the wildlands are critical in cities as well, a presumption that could be evaluated through the complementary use of the methods such as space-for-time substitution as well as methods that incorporate elements of professional opinion regarding tree adaptability (e.g., Brandt et al., 2016, and the professional opinion filter in this study).

5. Assumptions and limitations of the study method

Our novel method, when applied to urban trees, relies on two notable assumptions, and suffers several inherent limitations. First, the cities being compared should have access to the same palette of trees, i.e., should not be dependent on locally-particular species (e.g., natives) that would be unavailable elsewhere. To evaluate whether there was/is a common set of tree suppliers to the cities in our study, we contacted three largest wholesale tree nurseries in California. All three confirmed that their municipal clients range from across California, i.e., that all the cities are choosing from the same species catalogs and could have selected the same tree species (D. Cox, D. Tauschler, H. S. Florez-Henderson; personal communications). In addition, it is evident from our tree species list – where the non-natives popular with cities across the US predominate – that the trees indeed were likely obtained from commercial sources. Furthermore, the cities in our study area are of relatively similar age (i.e., their urban forests were planted starting in the mid-20th century), which reduces the chance of having the results skewed by trends in urban tree species selection, but perhaps limits the scope of inference. We note that these characteristics – common market for trees, common age of cities – are unlikely to be replicable in every geographic context.

Second, the method presumes that the absence of a species is caused by its inability to survive the warmest season, rather than other causes, e.g., aesthetic preference of the local tree manager. While it is impossible to conclusively rule out these other causes, our sampling method inherently selects only the very common trees in each city, and it is the ubiquity of these species that makes their absence from a city unlikely to be caused by factors other than climatic incompatibility. To further assess the commonness of the species we encountered, we searched the species listed as common in the "State of Urban Forestry in California" reports (Thompson and Reimer 2017, unpublished data; Thompson, 2006), and fewer than 20% (n = 10) of the species listed in Table 3 are missing from the Thompson reports, i.e., could be considered not-quite-ubiquitous across California, while still being locally common and locally available for planting (if they were climatically suitable).

However, while reliance on ubiquitous species likely ensures that the method meets the "species absence as evidence of climatic incompatibility" assumption, it also reveals a limitation of the method: namely, the results are likely to be un-informative regarding many less-common trees, even though such trees could be well-adapted for the future warm climate. In other words, our method cannot answer the question whether an uncommon species, absent from the sample, will perform well in the changing climate.

A second notable limitation of the method is the possibility that a warm city could *today* have minimum winter temperatures that are lower than those in the representative city, resulting in the absence of

some frost-tender tree species from the warm city and thus potentially misleading results. In this study, five of the cities used as comparison (warm) cities are in colder hardiness zone than corresponding representative city: King City (compared to Santa Monica); Santa Ana (compared to San Diego); Fresno (Burbank); Barstow (Riverside); and Furnace Creek (El Centro; http://planthardiness.ars.usda.gov/PHZMWeb/). This potential problem can be ruled out for the Santa Monica/King City and San Diego/Santa Ana comparisons, as all of the common street trees the two example cities were found in their corresponding or warmer cities (which included cities in colder hardiness zones). For the other three example cities (Burbank, Riverside, and El Centro), we identified the frost hardiness tolerance for the common street tree species, and compared each to the hardiness zones of the warm city. Only 1 species in each representative city was identified as being potentially absent from the "warm" city because of low temperature. These were *Cassia leptophylla* (Fresno), *Lophostemon confertus* (Barstow), and *Acacia dealbata* (Furnace Creek). Thus, while this effect is insubstantial in the present study, it points to a limitation of the study method, and the need to consider the winter climate of each warm city under comparison.

Finally, the third notable limitation is in the necessity to find a comparable pair (warm equivalent) for each city under study. Although we were able to identify nearly ideal future-climate substitute cities for all our representative cities, this is a situation which may not be replicable in other areas, either because they are less urbanized (i.e., no city can be found having the necessary future climate), or because the ages of the cities differ widely (and thus would their history and palette of urban tree species).

This study provides the first evidence that in some California cities a substantial portion of the usually-planted street tree species are unlikely to persist with the changing climate. Although not the first appearance of the space-for-time substitution method to analyze plant responses to climate change (see e.g., Broadmeadow et al., 2005, and Blois et al., 2013) to our knowledge this is the first study applying this method to urban forestry, and demonstrates its potential usefulness as complement to other approaches of evaluating climate change effects in cities. This is because urban forests differ from wildlands not only in their environmental conditions, but also in that both the planting and removal of trees is controlled by human decisions, thus making it challenging to apply in cities the standard ecological methods used to predict climate change effects on vegetation. More research in this area is clearly needed, because although the area covered by cities is small, the proportion of the human population that will be affected by changes in the urban forests is large.

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